

LITTERFALL OF THE EXOTIC ACACIAS IN THE SOUTH WESTERN CAPE

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ABSTRACT

The annual litterfall of four species of Australian acacias naturalised in the Cape comprises 60 % foliage and 30 % reproductive structures and averages 704 g/m² (dry mass). While litter production of this magnitude is typical of subtropical Eucalypt forests, it is more than double the value recorded in evergreen scrub communities in winter rainfall regions. The ground beneath acacia thickets is covered by a layer of litter which has a dry mass per unit area equal to three times that of the annual litterfall, and which, according to the literature, is rich in phosphorous and has a low C/N ratio. Plants adapted to low nutrient levels do not compete successfully on fertilised soils (Specht, 1963), and it is suggested here that, by enriching the soil, acacias make the environment less suitable for indigenous Fynbos plants.

UITTREKSEL

PLANTE-AFVAL VAN UITHEEMSE ACACIAS IN DIE SUID-WESTELIKE KAAP

Die jaarlikse plante-afval van vier Australiese *Acacia*-soorte wat in die Wes-Kaap genaturaliseer het bestaan uit 60 % blaar- en 30 % voortplantingsstruktuur-reste met 'n gemiddeld van 704 g/m² (droë massa). Hierdie plante-afval produksie is tipies van subtropiese *Eucalyptus*-bosse maar meer as twee keer die waarde aangeteken vir immergroen struikgemeenskappe in winterreënvalstreke. Die grond onder *Acacia*-bosse is bedek met 'n laag plante-afval wat 'n droë massa per eenheid area het wat drie keer dié van die jaarlikse plante-afval is, en wat, volgens die literatuur, ryk is aan fosfor en met 'n lae C/N verhouding. Plante wat aangepas is vir 'n lae voedingsvlak kompeteer nie suksesvol op bemeste grond nie (Specht, 1963), en dit word voorgestel dat deur die grond te verryk, die acacias die omgewing minder geskik maak vir inheemse fynbos.

INTRODUCTION

A number of species of exotic Australian acacias are replacing the Fynbos and coastal shrub communities of the south western Cape, South Africa (Hall, 1979). The indigenous vegetation is dominated by small-leaved, sclerophyll, evergreen shrubs, and in structure resembles heathland and some shrubland in regions with mediterranean-type climates (Beadle, 1966; Loveless, 1962; Specht, 1963). The low productivity of the indigenous vegetation is indicated by its low biomass (Kruger, 1977), long lived leaves (Kruger, 1979) and the paucity of plant litter on the ground (Kruger, 1977). The exotic acacias are taller and faster

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growing and produce more litter than most indigenous plants and within a few years have overtopped the natural vegetation, and have covered the ground with a thick carpet of phyllodes, pods and twigs.

The aim of this paper is to compare the litter production and accumulation rate of exotic acacia thickets with that of sclerophyllous vegetation types similar to Fynbos. Hypotheses relating to the differences in productivity and nutrient turn-over of exotic and indigenous vegetation, which arise from this comparison, can be tested when the litterfall studies at present being carried out as part of the Fynbos Biome research programme (Anon., 1978) have been completed.

METHODS

All the data used in this paper were collected in mature, self-established thickets of exotic acacias on the Cape Peninsula and the adjacent Cape Flats between March, 1977 and November, 1978. They provide a quantitative assessment of the masses of the canopy, the annual litterfall and the ground litter.

Canopy mass

Nine *Acacia cyclops* Cunn. ex G. Don. and seven *A. saligna* (Labill.) Wendl. trees of various stem diameters were measured, felled, divided into foliage, twigs and branches exceeding 20 mm in diameter, and then weighed in the field. Each of the components was subsampled, and the dry/wet weight ratio of the sub-sample was used to estimate the dry weight of the entire tree. The mass of the canopy per unit area (i.e. excluding wood and branches over 20 mm in diameter) was calculated from equation (1).

$$\text{canopy mass (g/m}^2\text{) per unit area} = \frac{\text{canopy mass of tree (g)}}{\text{canopy area of tree (m}^2\text{)}} \dots\dots (1)$$

Canopy cover was assumed to be continuous. Total biomass per hectare was the product of total tree mass and tree density per unit area.

Annual litterfall

Ten terylene mesh bags attached to wire hoops 0.5 m diameter and mounted on iron fence droppers were arranged at random in thickets of each of the following acacia species, to catch falling litter: *A. cyclops*, *A. longifolia* (Andr.) Willd., *A. melanoxylon* R.Br. and *A. saligna*. Litter was collected at monthly intervals between May, 1977 and April, 1978, dried at 90 °C for 24 hours and weighed. The standard error on the mean monthly weight of the litter of each species never exceeded 10 %, so that the sum of the monthly means is considered to be a good estimate of the litter production of selected acacia thickets over the 12 month study period.

Ground litter layer

Ground litter was sampled during the winter of 1978. All litter within ten random 1/16 m² quadrats in each thicket was collected, dried and weighed. Although the distribution of the litter was sometimes patchy due to molehills and depressions on the ground, the mean for each study site is used as an estimate of the dry weight of the litter layer at steady state for a particular species.

Decomposition rate

This was not studied in the field, but was calculated from the litterfall and litter layer data, using Olson's (1963) equation (2).

$$K = L/X_{ss} \dots\dots\dots (2)$$

where L = annual litterfall (g/m²); X_{ss} is the litter on the ground at steady state, inclusive of the current year's litterfall (g/m²); and K is the decomposition constant.

The time taken for 95 % of the steady state litter to accumulate or to decay was estimated with the use of equation 3 (Olson, 1963).

$$3/K = T_{95 \%} \dots\dots\dots (3)$$

where K is the decomposition constant, and $T_{95 \%}$ decay or accumulation time.

RESULTS

Biomass of acacia thickets in the south western Cape (Table 1) is about ten times greater than that of mature Fynbos (11–26 t/ha dry mass: Kruger, 1977; Kathan, unpubl. data) and shrublands in other regions with mediterranean type climates (15–30 t/ha dry mass: Mooney, 1977). Like other evergreen shrubs (Mooney, 1977; Chapman, 1967), acacias lose about 10 % of their standing crop annually as litter, most of which is derived from the canopy (Table 1), but the actual mass of the litterfall per unit area is 3–4 times greater in acacia thickets than in low heath and shrub communities in mediterranean regions, since the acacias have a larger total biomass.

In a mature healthy thicket, very little of the acacia litter is woody. Phyllodes constitute the bulk of the litter (Table 2), while flowers, pods and seed together contribute about 30 % to the total annual dry mass of the litterfall. Twigs and caterpillar fras are variable, minor components. About half of the canopy mass is renewed annually. The litter accumulates on the ground, and in a mature thicket, the dry mass of the ground litter per unit area exceeds that of the living canopy (Table 1).

TABLE 1.

Litterfall and litter layer of *A. cyclops* and *A. saligna* compared with the total biomass and canopy masses of these species in the south west Cape.

	<i>A. cyclops</i>	<i>A. saligna</i>
Biomass (t/ha dry mass)	131 (4) ¹	135 (10) ¹
Litterfall as % of biomass	7,4	6,0
Litter layer as % of canopy mass	21,2	15,5
Canopy mass (t/ha dry mass)	22 (18)	12 (21)
Litterfall as % of biomass	43,5	68,0
Litter layer as % of canopy mass	125,0	177,3

¹: % error on mean is given in parenthesis

TABLE 2.

Components of annual litterfall of exotic acacias in the south-western Cape

Components	<i>A. cyclops</i>	<i>A. longifolia</i>	<i>A. melanoxylon</i>	<i>A. saligna</i>
Total litter (g/m ²)	968	543	503	804
Flowers %	1,4	10,6	6,7	8,7
Pods %	35,5	16,0	0,5	12,1
Seed %	5,3	8,3	0,3	8,0
Twigs %	11,3	2,6	26,5	10,0
Unident. & fras %	7,7	0,8	2,7	10,4
Phyllodes % ...	39,0	61,7	63,3	60,8

The annual litter fall of the four species studied (averaging 704 ± 110 g/m²/p.a.) is comparable with that of forests in the sub-tropical and warm temperate regions of south east Queensland, New South Wales, Victoria and South Australia (400–800 g/m²/p.a.: Rogers & Westman, 1977; Maggs & Pearson, 1977; Attiwill, 1968; Ashton, 1975; Ashton & Frankenberg, 1976). The litterfall of evergreen scrub communities in mediterranean type climatic regions is about 200 g/m²/p.a. (Mooney, 1977; Specht & Rayson, 1957), which falls short of the averages for warm temperate (550 g/m²/p.a.: Bray & Gorham ex Birk, 1979) and even cool temperate regions (300–400 g/m²/p.a.: Kozlowski, 1973). This low productivity has been attributed to the summer drought which limits photosynthesis, and to the poverty of the soils (Mooney, 1977; Specht, 1973). The south western Cape, where high productivity acacias are replacing low productivity heath- and shrubland, without the assistance of artificial fertilisers, provides a natural experiment for the study of differences in the growth and nutritional strategies of these plants.

The ground litter layer of the acacia thicket weighed between 1 400 and 2 800 g/m², which is fairly average by world standards, but greatly exceeds the

99–495 g/m² recorded in mature mountain Fynbos (Kruger, 1977). That there is a marked difference in the accumulation of litter under exotic acacias and indigenous vegetation is clearly seen in the field. Under acacia thickets, the litter layer forms a carpet 20–40 mm deep, unbroken except where disturbed by moles. Under Fynbos and other indigenous communities, the litter is thin and patchy. Litter covers an average of 15 % of the soil surface under Fynbos on Table Mountain, Cape Peninsula ($n = 31$; Glyphis, 1976), 12 % under coastal bush ($n = 50$; S. J. Milton, unpubl.) and 5 % under the dry Fynbos on Piquetberg, south western Cape ($n = 36$; H. P. Linder, unpubl.).

The mass of the annual litterfall of acacias in the south western Cape was equal to about one third of the mass of the ground litter, giving the decomposition constant a value of between 0.326 and 0.384. When litterfall and ground litter dry weights of the exotic acacias are plotted on Olson's (1963) graph (Fig. 1) which shows the relationship between these parameters for a wide range of

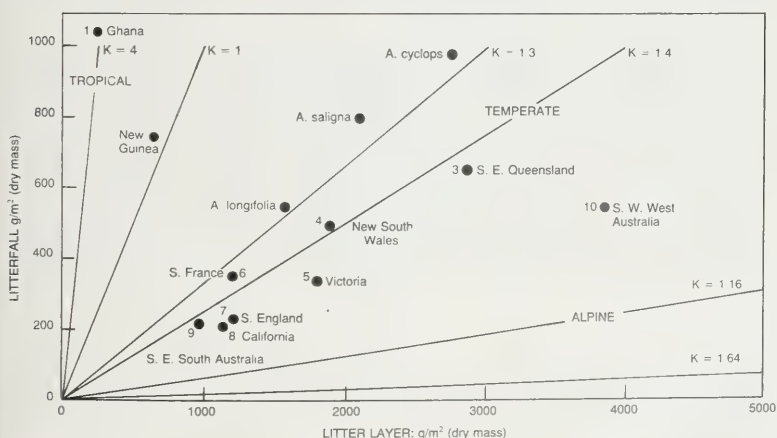


FIG. 1.

Decomposition rates of the litter of exotic acacia thickets in the South western Cape compared with those of other plant communities, world wide. The decomposition rate is represented by the slope of the line (K). The figure is based on that of Olson. (1963), and the points plotted represent K values given in the following papers:

- | | | |
|------|-----------------------------------|----------------------|
| 1, 2 | : Edwards, 1977 | (Tropical forest) |
| 3 | : Rogers & Westman, 1977 | (Eucalypt forest) |
| 4 | : Maggs & Pearson, 1977 | (Coastal scrub) |
| 5 | : Attiwill, 1968 | (Eucalypt forest) |
| 6 | : Lossaint, 1973 | (Dry Quercus forest) |
| 7 | : Chapman, 1967 | (Heath) |
| 8 | : Mooney, 1977 | (Chaparral) |
| 9 | : Lee & Correll, 1978 | (Sclerophyll forest) |
| 10 | : Hatch ex Rogers & Westman, 1977 | (Eucalypt forest) |

plant communities, the slope of the line (K) lies realistically between the lines for tropical regions (which can exceed 1,00) and for temperate regions (about 0,25).

The time taken for 95 % of the steady state litter to accumulate or to decompose was estimated from equation 3. The estimated value of between 7 and 9 years for exotic acacias in the south western Cape is faster than the decomposition rate in temperate and boreal conifer forests or in Chaparral (Olson, 1963; Mooney, 1977). Kruger's (1977) data show that litter under Fynbos may have reached equilibrium within six years: but, even if Fynbos litter were to decay as rapidly as it fell (which is unlikely in a mediterranean-type climate) this would not account for the paucity of the litter layer. As in other mediterranean scrub communities, the lack of litter on the ground under Fynbos must be attributed to very low litterfall values.

DISCUSSION

The nitrogen and phosphorous content of the foliage of Australian acacias (Ashton, 1975; Everist, 1969) exceeds that of sclerophyll vegetation on nutrient poor soils (Lossaint, 1973; Maggs & Pearson, 1977; Lee & Correll, 1978) and is 2-4 times as great as that of Fynbos plants (A. B. Low, unpubl. data). This difference is also reflected in the protein content of acacia shoots ($15,2 \pm 1,0$ %: Everist, 1969) which is about three times as high as that of browseable shrubs sampled in plant communities in the Fynbos Biome: 3,5-6,0 % (Joubert & Stint, 1979). Since the average annual litterfall of the exotic acacias is also three times as great as values cited for mediterranean scrub types (Fig. 1), the annual nitrogen and phosphorous input by acacia litter should be about nine times as great per unit area, as that of Fynbos.

Assuming a nitrogen content of 1,5 % and a phosphorous content of 1,13 %, acacia litter would contribute $10,5 \text{ g/m}^2 \text{ N}$ and $0,92 \text{ g/m}^2 \text{ P}$ to the soil each year, as compared with $1-3 \text{ g/m}^2 \text{ N}$ and $0,03 \text{ g/m}^2 \text{ P}$ in Garrigue, Chaparral and South Australian sclerophyll forest (Loissaint, 1973; Mooney & Parsons, 1973; Lee & Correll, 1978).

The rapid decomposition of acacia litter (7-9 years) as compared to the 13-15 years taken for 95% of the litter of sclerophyll scrub types to decay, might be explained by the fact that the low C/N ratio of acacia litter favours microbial activity (Birk, 1979; Ashton, 1975).

Apart from the nitrogen added to the soil by the litter, the activity of the symbiotic bacteria in acacia nodules fixes nitrogen, changing the soil nitrogen status (Nakos, 1977; Langkamp *et al.*, 1979). The total input of nitrogen to an *A. mearnsii* plantation has been estimated to be in the order of $20 \text{ g/m}^2/\text{p.a.}$ (180 lb/acre/p.a. ; Hallsworth, 1958). Acacias, probably due to the presence of mycorrhiza, are also able to accumulate phosphorous (Barrow, 1977).

There is evidence that the addition of nutrients to oligotrophic, sclerophyll

ecosystems increases their growth rate thereby upsetting the water balance of the plant community and killing species with strong summer growth rhythms (Specht, 1973). This results in the opening up of the sclerophyll community, and an increase in the number of annuals and spring-growing exotic perennials (Specht, 1963, 1973). It follows that Fynbos communities, which also have a summer growth rhythm (J. Sommerville, unpubl.; Kruger, 1979), are found on some of the most nitrogen and phosphorous deficient soils in the world (A. B. Low, unpubl. data) and probably conserve nutrients by storage and internal cycling (Specht, 1963; Kruger, 1979). Such stress-tolerant plants would not be expected to compete successfully on a nutrient enriched soil (Grime, 1977). The prevalence of grasses (indigenous and exotic) on areas recently cleared of acacias may be further evidence for the change in the soil nutrient status which acacias effect.

CONCLUSION

Their evolution in a temperate climate, their early and extended growing season, their tall growth habit and their freedom in the Cape from effective predators and pathogens, have all contributed to the success of the Australian acacias in the Fynbos biome (Milton, 1980). This paper suggests that another important factor in favour of the acacias is their ability to maintain a high rate of litterfall and litter turn-over, and by so doing to boost the nitrogen and phosphorous status of the soil. This nutrient enrichment may be one of the factors enabling the exotic acacias, once introduced to an area, to maintain a hold among indigenous shrubs, and eventually to change, degrade and replace the original Fynbos vegetation.

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